Journal of Experimental Psychology: General

Planning-Related Motor Processes Underlie Mental Practice and Imitation Learning

Patric Bach, Bassem Khalaf Allami, Mike Tucker, and Rob Ellis

CITATION

Planning-Related Motor Processes Underlie Mental Practice and Imitation Learning

Patric Bach, Bassem Khalaf Allami, Mike Tucker, and Rob Ellis
University of Plymouth

It is still controversial whether mental practice—the internal rehearsal of movements to improve later performance—relies on processes engaged during physical motor performance and, if so, which processes these are. We report data from 5 experiments, in which participants mentally practiced complex rhythms with either feet or hands while using the same or different body parts to respond to unrelated sounds. We found that responses were impaired for those body parts that were concurrently used in mental practice, suggesting a binding of body-part-specific motor processes to action plans. This result was found when participants mentally trained to memorize the rhythms, to merely improve their performance, when mental practice and execution directly followed one another and when separated by a different task. Finally, it was found irrespective of whether participants practiced on the basis of a symbolic rhythm description and when they practiced by watching somebody perform the rhythms (imitation learning). The effect was eliminated only when the requirement for mental practice was eliminated from the task while keeping visual stimulation identical. These data link mental practice not to execution but planning related motor processes and reveal that these planning processes underlie both mental practice and imitation learning.

Keywords: mental practice, action planning, imitation, observation learning, stimulus–response compatibility

Supplemental materials: http://dx.doi.org/10.1037/a0035604.supp

Mental practice—the internal rehearsal of movements to improve their later performance—underlies the development and the execution of many of our motor skills. It often directly precedes action execution and takes the form of an explicit act of motor planning ("preperformance imagery;" Morris, Spittle, Watt, & Fletcher, 2005). Platform divers may take a few seconds to visualize their movements before jumping off, or weightlifters may visualize the ideal weight distribution relative to their gravity center. In addition, mental practice can be used "offline" to play through behaviors the athlete will perform much later, often in circumstances that bear no similarity to the actual performance situation. For example, former England goalkeeper David James reported that he would engage in mental practice whenever possible: Even when stuck in traffic, he would "do a few crosses in his mind" (Winter, 2002).

Both forms of mental practice are effective across a broad range of skills, ranging from simple manual movements to expert athletic performance, such as diving, swimming, or golf (e.g., Grouious, 1992; Noel, 1980; for meta-analyses, see Feltz, Landers, & Becker,

1988; Hinshaw, 1991). Mental practice helps automatizing motor skills and may, in some cases, have stronger effects than physical practice (Wohldmann, Healy, & Bourne, 2007; 2008). More than 90% of professional athletes now incorporate mental practice in their training regimes (Jowdy, Murphy, & Durtschi, 1989), and it is increasingly used in other fields as well, such as surgery or music education (e.g., Arora et al., 2011; Ross, 1985; Zimmermann-Schlatter, Schuster, Puhan, Siekierka, & Steurer, 2008). It appears to be particularly effective when supported by video demonstrations of the skill (e.g., Hall & Erffmeyer, 1983), suggesting a link between mental practice and observational learning.

A core question is why mental practice has these beneficial effects. Early conceptions have understood mental practice as an abstract, symbolic process, such as "the symbolic rehearsal of a physical activity in the absence of any gross muscular movements" (Richardson, 1967, p. 95). In such views, the benefits emerge because mental practice supports cognitive (re)structuring of the action plans, facilitates access to the different nodes in their hierarchical structure, or facilitates the chunking and coordination of action units (e.g., Driskell et al., 1994; Minas, 1978; Sackett, 1934; Weigelt, Ahlmeyer, Lex, & Schack, 2011). Indeed, meta-analyses have revealed that mental practice has larger effects on tasks with a strong cognitive component compared to purely motor tasks (e.g., Feltz & Landers, 1983; Hird, Landers, Thomas, & Horan, 1991; Ryan & Simons, 1983). However, more recent research has challenged these ideas, revealing that mental practice can also directly affect core motor and physiological variables of performance. For example, Wohldman et al. (2007, 2008) revealed

Patric Bach, Bassem Khalaf Allami, Mike Tucker, and Rob Ellis, School of Psychology, University of Plymouth, Devon, United Kingdom.

Bassem Khalaf Allami was supported by Mustansiriya University, Baghdad, Iraq.

Correspondence concerning this article should be addressed to Patric Bach, School of Psychology, University of Plymouth, Drake Circus, Devon PL4 8AA, United Kingdom. E-mail: patric.bach@plymouth.ac.uk

a direct impact on the execution (rather than planning) stages of action. Roure et al. (1999) revealed that changes in heart rate during mental practice predicted subsequent improvement in volleyball. Perhaps most strikingly, purely mental practice of finger and arm movements is enough to improve the physical strength of these movements (Reiser, Büsch, & Munzert, 2011; Yue & Cole, 1992).

Such physiological effects are hard to explain by purely symbolic accounts of mental practice. It has therefore been proposed that mental practice of motor skills is at least partially "enactive" and rooted in the processes guiding physical motor execution. Accordingly, mental practice is based on visual and kinesthetic motor imagery that "simulates" the sensory input that would occur during physical execution (e.g., Decety, 1996; Jeannerod, 2001). These simulations are assumed to make use of processes that occur, in very similar form, during the physical performance of the actions. For example, it has been proposed that a "subliminal activation" of the motor apparatus would evoke the sensations associated with action execution and allow actors to mentally rehearse the actions (e.g., Jacobson, 1930; Jeannerod & Frak, 1999). Newer accounts assume that they emerge from internal models that, during action execution, generate visual and kinesthetic predictions of movement outcomes (e.g., Grush, 2004; Wolpert & Flanagan, 2001; for related proposals, see Annett, 1995; Jeannerod, 1995; Vogt, 1996).

Evidence for enactive accounts comes mostly from studies investigating motor imagery outside of a mental practice context. Studies have shown that motor imagery is accompanied by subtle activity in those muscles that are typically used to perform the movement, consistent with Jeannerod and Frak's (1999) idea of subliminal motor system activation (Jacobson, 1930; see Guillot et al., 2007, for more recent findings). Moreover, the timing of mental imagery closely follows the timing of the actual movements (e.g., Decety & Michel, 1989; Georgopoulos & Massey, 1987; Landauer, 1962; Mackay, 1981; Steggemann, Engbert, & Weigelt, 2011; but see Reed, 2002), and people's ability to mentally rotate body parts depends on these body parts not being concurrently engaged in another movement (e.g., Ionta, Fourkas, Fiorio, & Aglioti, 2007; Wohlschläger & Wohlschläger, 1998). A host of neurophysiological studies shows that imagery of movement goes along with activity in brain regions involved in motor control and planning, such as the premotor and motor cortices, the supplemental motor areas, as well as the parietal lobe (e.g., Miller et al., 2010; Naito et al., 2002; Porro et al., 1996; for reviews, see de Lange, Roelofs, & Toni, 2008; Lotze & Halsband, 2006). Finally, similar motoric activations have been observed when people watch others act, prompting the idea that the same motor processes are engaged during action observation and observational learning (e.g., Brass, Bekkering, Wohlschläger, & Prinz, 2000; Chartrand & Bargh, 1999; for a review, see van der Wel, Sebanz, & Knoblich, 2013).

Despite this broad support for enactive theories of motor imagery, the involvement of motor processes in mental practice is still debated. One reason is that most of the data discussed above came from studies investigating motor imagery outside a mental practice context, where motor imagery was not used with the goal to improve subsequent motor performance. In addition, even the data on motor imagery outside of a mental practice context is far from equivocal and leaves many questions unanswered. Several studies

suggest that motor activity during imagery is primarily found when participants imagine themselves from the first-person, rather than the third-person, perspective, and when they are instructed to focus on the actions' kinesthetic sensations rather than just their visually perceivable effects (e.g., Lorey et al., 2009; Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006). Often, these forms of mental practice require explicit training and are not spontaneously used by participants (e.g., Lotze et al., 1999). Motor involvement during motor imagery and mental practice may therefore be far from a general phenomenon but may be restricted to specific circumstances.

Even in cases of kinesthetic egocentric imagery, various studies report either only very transient or complete absence of actual motor (rather than premotor) activation (e.g., Dechent, Merbold, & Frahm, 2004; Macuga & Frey, 2012; for a review, see Lotze & Halsband, 2006), or even striking dissociations (e.g., Hanakawa, Dimyan, & Hallett, 2008; Reed, 2002). As an instructive example, amputees sometimes report the feeling of being able to control their phantom-limbs, a phenomenological experience that contrasts starkly with—and appears more "real"—than imagery of movement. A neuroimaging study confirmed this dissociation, with brain activity during phantom-limb movements being virtually identical with actual movements, but strikingly different to imagined movements (Raffin, Mattout, Reilly, & Giraux, 2012). This indicates that motor execution and imagery do dissociate, even when the actual movements and the kinesthetic feedback are controlled.

Finally, even in studies that do report motor activation, it is often not clear what the role of this activation is, the evidence being subject to various interpretations. First, it has been argued that the observed motor effects during action simulation are purely epiphenomenal—a downstream consequence brought about by associations between cognitive control and motor areas—rather than the basis of mental practice processes (for discussion, see Jeannerod, 1994; Mahon & Caramazza, 2008). Second, the possibility has been raised that the reported motor activations may reflect action planning processes rather than execution processes (e.g., Hanakawa et al., 2008), a suggestion further supported by the more robust involvement of premotor rather than motor cortices in motor imagery (for a review, see Lotze & Halsband, 2006). And third, they may reflect the *inhibition* of motor output, rather than an *excitation* of the relevant motor structures, and data from an fMRI functional connectivity study indeed reveals an inhibitory influence of action planning areas onto the motor cortex (Solodkin et al., 2004).

The Present Study

The aim of the present study is to develop a behavioral paradigm that allows us to directly investigate the mechanisms underlying mental practice and to resolve some of the above questions. It has three main goals. The first goal is to provide a first behavioral test of whether mental practice engages processes involved in the physical execution of motor skills. Importantly, this should be demonstrated in a task that has sufficient motor complexity to benefit from mental practice but in which participants neither have to be instructed nor trained in a specific form of imagery (first-person kinesthetic), which is known to create an inherent bias toward motor engagement but which may not be naturally used by

participants. The second goal is to resolve the functional role of this motor activation. Is it facilitatory or inhibitory? Does it reflect the simulated execution of the action, or is it better conceptualized in terms of action planning? The third and final goal is to compare this motor activation during mental practice to motor activation during observation learning. As noted, a large body of research suggests that the observation of action goes along with a similar subliminal motor activation as motor imagery and that this motor activation might be the foundation for the later imitation of the observed actions (for a review, see Iacoboni, 2009). An important question is therefore if both—mental practice and imitation learning—are based on the same underlying mechanisms. Demonstrating such a similarity would allow one to conceptualize learning from observing others (i.e., imitation) in the same way as mental practice of action.

We adapted the well-established stimulus–response compatibility (SRC) task. SRC tasks are typically used to investigate whether overt, visual stimuli directly affect motor output. For example, in the classic Simon task, participants are faster to respond with the left hand to a stimulus on the left, and with the right hand to a stimulus on the right, even when stimulus laterality is task irrelevant (Simon, 1969; Simon & Rudell, 1967; for review, see Hommel, 2010). Such effects are typically taken as evidence that the mental activation of a stimulus feature activates planning and execution related processes. Similar effects have now been observed for various stimulus and response types, such as hand/object orientation, object/grip size, and shape/hand trajectory (Bach, Griffiths, Weigelt, & Tipper, 2010; Craighero, Fadiga, Rizzolatti, & Umilta, 1999; Tucker & Ellis, 2001). They are also found when people see, imagine or read about action (e.g., Bertenthal, Longo, & Kosobud, 2006; Brass et al., 2000). Such effects can be very general, affecting whole effector systems. For example, seeing actions with hands or feet facilitates responding with the same body parts, even when the actual movements to be executed with these body parts are different (Bach, Peatfield, & Tipper, 2007; Bach & Tipper, 2007; Gillmeister et al., 2008).

Our study adapts this paradigm to probe the state of the motor system while people mentally practice complex rhythms in order to improve their subsequent performance. In the first half of each trial, participants were presented with symbolic descriptions of complex rhythms (ABABB . . . ; see Figure 1, left panel, for an example). They were instructed to mentally practice these rhythms with either their hands or their feet (while keeping completely still), in order to fluently reproduce them in the second half of each trial (using the same body parts). While they mentally practiced the rhythms, one of two sounds was played to participants, which required them to respond with either a key-press of their hands or a key-press of their feet. These key-presses are unrelated to the main task of mentally practicing the rhythms, but involve either the same or different body parts. They therefore allow us to probe whether mental practice engages the foot- and hand-specific motor pathways utilized during physical execution. If this is the case, then the efficiency of these unrelated hand or foot responses should depend on whether participants simultaneously used these body parts for mentally practicing the rhythms.

Such an effect can take one of two forms. First, as is the case for many prior studies investigating perception–behavior links (e.g., Bach et al., 2007; Brass et al., 2000; Simon & Rudell, 1967), using a body part for mental practice might *facilitate* responding with
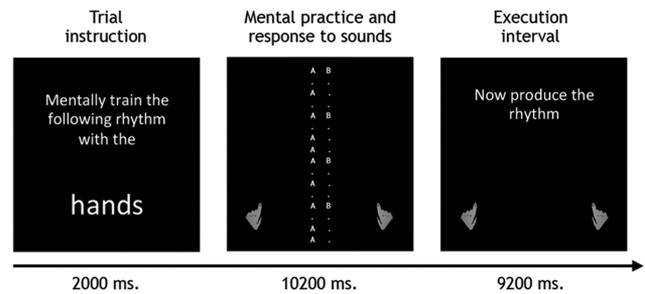

Figure 1. Illustration of the trial sequence. The trial instruction (left panel) informed participants about the body part they had to mentally practice the rhythm with. They then mentally trained the rhythm (middle panel). While they mentally practiced, one of two sounds was played (5,000; 5,500; 6,000; or 6,500 ms into the mental practice interval). Participants responded to the sounds with button presses either using their hands or their feet. After mental practice, another instruction appeared that prompted them to execute the rhythm from memory (right panel).

this body part to the sounds. Such a finding would support the idea that mental practice engages processes similar to the actual execution of the rhythms. In particular, it would support the idea that mental practice leads to a subtle activation of the motor programs or the muscles used in the trained action, which primes responses with these body parts (cf. Jacobson, 1930; James, 1890; Jeannerod & Frak, 1999; Thomaschke, Hopkins, & Miall, 2012).

Second, however, mental practice with a body part could also *impair* the usage of the body part for other responses. Such an outcome might appear particularly likely if one assumes that mental practice specifically engages planning, rather than execution-related motor processes. There is now considerable evidence that action planning involves selecting the sensory features the action should have to achieve its goal: how it would look, sound, and feel if it were successful (cf. Hommel, 2013; Hommel, Müsseler, Aschersleben, & Prinz, 2001). Actors may specify, for example, the speed, direction and the trajectory of the intended movement, or, in our case, the sequence of left and right button presses, and which body part they have to be executed with. These intended features do not only serve as goal states for motor production but also allow the action to be monitored once it is underway and provide effective error signals (for a review, see Hughes, Desantis, Waszak, 2012). Converging evidence indicates that, as soon as such a selection is made, the underlying codes become "bound" to the action plan until it is executed and are, in the meantime, less available to other processes, perhaps to shield them from interference (for reviews, see Hommel et al., 2001). It has been found, for example, that merely planning a specific movement (i.e., a button press on the left side) makes it harder to execute responses—and even to perceive stimuli—that have the same features as this planned response (e.g., detecting stimuli on the left or using other body parts on the left side; Müsseler & Hommel, 1997; Stoet & Hommel, 1999; for a review, see Thomaschke et al., 2012). Importantly, these effects are planning and not execution-related: They are found as long as an action is planned but disappear after it is physically executed (e.g., Wühr & Müsseler, 2001).

Similar effects are known from the task-switching literature. If a participants' goal stays the same between trials, they find it easier

to repeat the same movement that they had just executed. If, however, their action goal changed, movements with different features are easier to execute (e.g., Schuch & Koch, 2004), again supporting the idea that action features are "bound" to specific action goals. Again, for these response-repetition costs to be observed, it is necessary that the prior movements were planned, not that they were physically executed (Hübner & Druey, 2006; Schuch & Koch, 2010). If mental practice is based on these action planning processes, then a similar linkage of responses to action plans should be found in the present experiments. Action planning accounts of mental practice therefore predict negative—rather than positive—compatibility effects: Mentally practicing a rhythm with the hand should impair one's use of the hands when responding to the sounds, and mentally practicing with the foot should impair responses with the foot.

Experiments 1 and 2: Immediate Reproduction

Experiments 1 and 2 provide a first behavioral test of whether mental practice of a motor skill relies on body-part-specific mechanisms involved in action execution. In every trial of these experiments, participants were first presented with a complex rhythm that they had to mentally practice with their hands or feet (while keeping completely still). In the second half of the trial, they then had to reproduce this rhythm as quickly and as accurately as possible, using the same body parts as during mental practice.

Our main goal was probing the state of the motor system while participants mentally practiced. We therefore interrupted participants' mental practice by playing one of two sounds, which prompted them to make speeded responses with either theirs hands or their feet. We investigated whether participants' ability to make these hand and foot responses was affected by whether the body parts were concurrently used in mental practice. As noted, such an effect can take one of two forms. If mental practice involves a subliminal activation of motor commands or muscles used in the action, then positive compatibility effects should be observed: Responses with the body parts that are used for mental practice should be easier than responses with a different body part. In contrast, if mental practice involves action planning processes and a binding of motor codes to action plans, then responses with a body part concurrently used in mental practice should be harder to make than responses with a body part not used in mental practice.

These predictions were tested, first, in a situation in which participants had to reproduce the mentally trained rhythms from memory, without any memory aids (Experiment 1). Nonrandom performance was therefore only possible if participants used mental practice to effectively memorize the movement sequences. The effects were then replicated in Experiment 2, where this requirement was somewhat relaxed. Here, mental practice was not used to memorize the rhythms but merely to improve their subsequent performance, similar to the typical use of mental practice in sports. A memory aid, which showed the correct sequence of taps, was therefore given in the execution interval. However, as the rhythms were difficult to play, satisfactory performance still required effective prior mental practice. (For confirmation of this assumption, see the online supplemental materials.)

Method

Participants. Twenty students (five male; age range: 18–27 years) took part in Experiment 1 and 23 (eight male; age range: 18–24 years) in Experiment 2. They satisfied all requirements in volunteer screening and gave informed consent approved by the School of Psychology Ethics Committee at Plymouth University (Devon, England). Participants were paid either at a rate of £6/hr or they received course credits. All participants were in good health, had no history of disease or medical treatment that might influence visuomotor functions. In these and all following experiments, participants were excluded when they produced invalid rhythms in the execution interval (rhythms 50% longer/shorter than the required rhythm length) or invalid responses to the tones (responses made before the tones were played, or responses for which the press of only one or no response key was detected) in more than 20% of the trials. These criteria therefore capture both aspects of successful task performance: rhythm production and responses to the sounds. Four participants in Experiment 1 and five in Experiment 2 were excluded based on these criteria.

Materials and apparatus. The experiments were controlled by the experimental control software Presentation (http://www.neurobs.com), running on a 2.0-GHz PC running Windows XP. Foot responses were recorded with two foot pedals (33 cm apart), which were attached to the floor with black tape, and connected to the computer via the parallel port. Hand response keys were the Ctrl key (operated by participants' left hand) and the Enter key on the number block (operated by the right hand). Sounds were played via an external loudspeaker system.

Twenty different rhythms were created. Ten of these rhythms were to be played with the left and right hands and 10 rhythms (mirror images of the first 10 rhythms) were to be played with the left and right feet. All rhythms were presented in a symbolic format consisting of 16 lines, each line corresponding to the click of an imagined metronome. The taps that participants had to produce were represented by A's on the left and B's on the right side of each line. A's on the left side represented button presses or foot pedal presses on the left side, while B's on the right side represented presses with the right foot or right key. A line containing both an A and a B designated taps with both feet or hands. To the left and the right of each rhythm, a symbol depicting either a hand or a foot was shown, reminding participants of the body part with which this rhythm would have to be mentally practiced and subsequently played.

Two sounds were used as cues for the participants' responses in the memorization/mental practice interval: a high sound (sine wave of 1,331 Hz) or a low sound (sine wave of 223 Hz). Both sounds lasted 100 ms and were faded in and out at the start and end.

Procedure and design. The participants were seated in a dimly lit room, facing a computer at a distance of approximately 60 cm. The experiments contained three training sessions that lasted about 20 min altogether, each consisting of eight trials. The experiment proper took about 36 min, resulting in a total experiment time of roughly 55 min. The participants were tested individually and instructed by the software and the experimenter.

The first training session introduced the participants to the (difficult) task of tapping the rhythms. In each of the eight trials, participants were first presented with a cue telling them which

effectors (hands or feet) they had to use to produce a rhythm. This cue remained on the screen for 2,000 ms and read "Produce the following rhythm with the hands/feet!" After a short blank (300 ms), the rhythm was shown on the monitor (see Figure 1, middle frame). Pictures to its left and right reminded participants of the body part to be used. Participants then produced this rhythm while it was on the screen (maximum 11,200 ms).

The second training session introduced participants to the mental training component of the task. In each trial, participants were again first presented (for 2,000 ms) with a cue specifying the body parts (hands or feet) they should use to mentally train the following rhythm (Figure 1, left panel). After a short blank (300 ms), they were then shown one of the 20 rhythms that they had to mentally practice for 10,200 ms, while not making any overt movement (Figure 1, middle panel). The rhythm description remained on the screen in this interval. After another blank (800 ms), a cue saying "Now produce the rhythm!" appeared. In Experiment 2 this was accompanied by the same symbolic rhythm description that was presented in the mental practice interval, while in Experiment 1 the remainder of the screen remained blank (Figure 1). Participants now played the rhythm from memory with the body part that was previously instructed. They were reminded of this body part with small pictures appearing on the screen (see Figure 1, right panel). They had 9,200 ms to tap the rhythm.

The third training session introduced participants to the secondary task (responding to the sounds) and was identical to the actual experiment (see Figure 1 for a schematic). The trials in the third training session were identical to the second training session, with the exception that low and high tones were played while partici-

pants mentally practiced (5,000; 5,500; 6,000; or 6,500 ms from the start of the mental practice interval). The participants' task was to press both foot pedals as quickly as possible when hearing the low tone, and both hand keys when hearing the high tone. As before, at the end of the mental practice interval, the rhythm disappeared and the cue that prompted participants to perform the rhythms appeared. As before, In Experiment 1, the rhythm itself was not presented again, requiring performance from memory. In Experiment 2, the same symbolic rhythm description as in the mental practice interval was displayed, and participants were instructed to maximize performance.

The trials in the actual experiment were identical to the third training session. There were 80 trials altogether, separated by short breaks every 20 trials. All rhythms were shown once per block. There were equal numbers of trials in which the rhythms had to be played with the hands or the feet, and equal numbers for responding to the sounds with hands or feet.

Analysis. The main analysis tested whether the foot and hand responses to the sounds depended on whether participants concurrently used these body parts for mental practice (see the post hoc analyses below the effects on subsequent rhythm performance). Error rates for the responses to the sounds were calculated for each participant and condition by dividing the number of incorrect responses (participants using a wrong body part to respond to the beep) by the total number of trials. Trials were excluded if participants responded too early (i.e., before the imperative tone stimulus) or if the press of both response devices was not detected (2.9% in total). Mean response times (RTs) were calculated as the average RT of the left and right response keys, additionally excluding
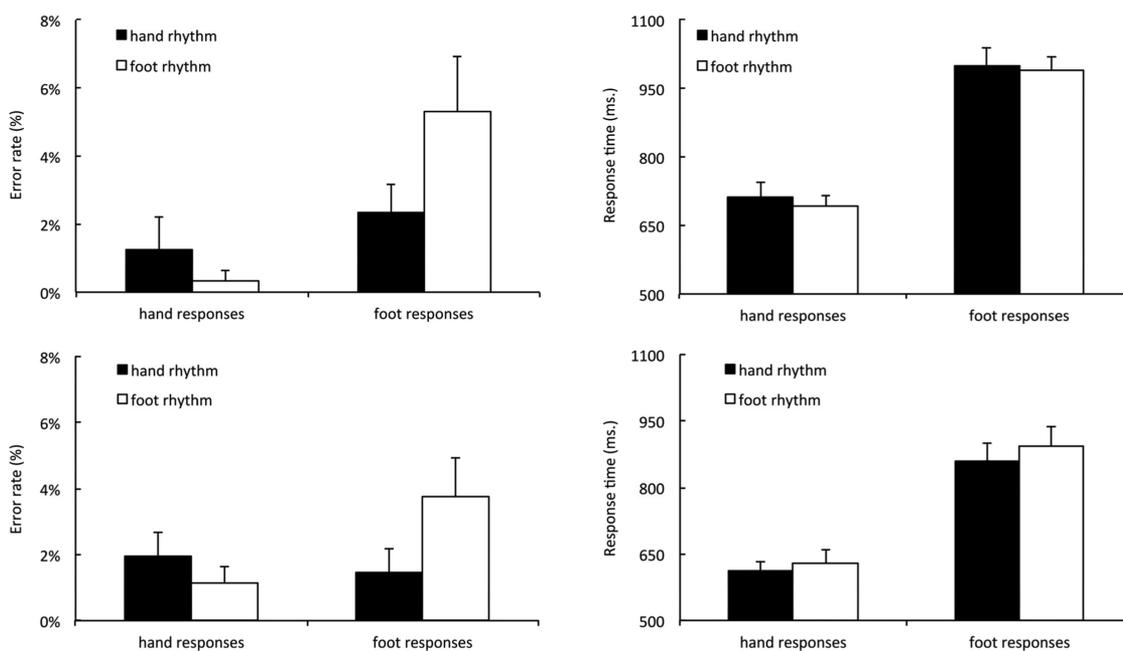

Figure 2. Error rates (left panels) and response times (right panels) for responses to the sounds in Experiment 1 (top row) and Experiment 2 (bottom row). In each panel, the two left bars show the data for responses with the hand, and the two right bars show responses with the feet. The black bars show responses while hand rhythms were mentally practiced, and the white bars show responses while foot rhythms were practiced. Error bars show the standard error of the mean.

error trials (2.1%) or trials in which the RT fell outside of three standard deviations of each participant's mean RT with this body part (0.2%).

Results

Participants' responses to the sounds while mentally practicing were analyzed separately for error rates and RTs with repeated-measures 2×2 analyses of variance (ANOVAs), with the factors Response Effector (foot, hand) and Imagery Effector (foot, hand). For Experiment 1 (Figure 2, top row), the analysis of error rates revealed no main effect of Imagery Effector, $F(1, 15) = 0.93$, $p = .352$, $\eta_p^2 = .06$, but a significant main effect of Response Effector, $F(1, 15) = 7.07$, $p = .018$, $\eta_p^2 = .32$. Participants made fewer errors when responding with the hand than with the foot. Importantly, the predicted interaction of Imagery Effector and Response Effector was significant, $F(1, 15) = 4.56$, $p = .045$, $\eta_p^2 = .23$, taking the form of an negative compatibility effect. Participants made more errors (and chose an incorrect body part) when the required body part was concurrently used for mental practice compared to when it was not used for mental practice (for separate analyses of each effector, see supplemental materials).

The analysis of the RTs similarly revealed a significant main effect of Response Effector, $F(1, 15) = 172.89$, $p < .001$, $\eta_p^2 = .92$, with faster responses with the hand than with the foot. There was no significant main effect of Imagery Effector, $F(1, 15) = 0.85$, $p = .370$, $\eta_p^2 = .05$, and, in contrast to the error analysis, no interaction, $F(1, 15) = 0.452$, $p = .511$, $\eta_p^2 = .03$. Importantly, there was no evidence for a speed accuracy trade-off. Numerically, responses were slightly faster when different body parts were used for response and mental practice. Moreover, when correlating the size of the compatibility effects in RTs and error rates, only a (nonsignificant) positive correlation emerged ($r = .10$), suggesting that, if anything, those participants with negative compatibility effects in the error rates also tended to show negative effects in the RTs.

Experiment 2 completely replicated this pattern of results (Figure 2, bottom row). Analysis of Error rates revealed neither a main effect of Imagery Effector, $F(1, 17) = 1.35$, $p = .262$, $\eta_p^2 = .07$, nor of Response Effector, $F(1, 17) = 2.19$, $p = .157$, $\eta_p^2 = .11$. However, the interaction of Imagery Effector and Response Effector again revealed a negative compatibility effect, $F(1, 17) = 7.37$, $p = .015$, $\eta_p^2 = .30$ (for separate analyses of each effector, see the supplemental materials). As before, the analysis of RTs only revealed main effects of Response Effector, $F(1, 17) = 87.7$, $p < .001$, $\eta_p^2 = .84$, and Imagery Effector, $F(1, 17) = 10.9$, $p = .004$, $\eta_p^2 = .39$, but no interaction, $F(1, 17) = 0.71$, $p = .411$, $\eta_p^2 = .04$. The compatibility effects in Experiment 2 were slightly positively correlated ($r = .10$).

Discussion

Experiments 1 and 2 tested whether mental practice of hand and foot actions affects the concurrent production of unrelated responses with the same body parts. The data revealed a negative compatibility effect: Participants made more errors when responding with the same body parts as those concurrently used for mental practice, compared to using different body parts. Thus, participants were more likely to accidentally respond with the foot when they were mentally practicing a rhythm with the hand, and more likely to accidentally respond with the hand when mentally practicing a rhythm with the foot.

This negative compatibility effect was found even though the rhythms were presented symbolically, and the task could in principle be solved by learning the sequence of button presses in an abstract, effector-independent manner. Moreover, it was obtained without first instructing participants in a certain type of imagery, which is known to produce inherent biases toward motor system activation (i.e., first-person imagery; e.g., Lorey et al., 2009; Stinear et al., 2006). Finally, all effects were replicated both when mental practice was explicitly required by the task to memorize the rhythms (Experiment 1) and when it merely served improvement of performance (Experiment 2), suggesting that they are general consequences of engaging in mental practice.

These data provide the first behavioral evidence that mental practice of rhythms spontaneously engages processes that are also involved in the execution of action, at least for tasks of sufficient motoric complexity such as ours. More specifically, the data suggest some form of resource competition, such that body parts involved in mental practice are less available for other, unrelated responses. This finding is consistent with the idea that mental practice engages action planning-related processes, which involve a binding of action features to motor plans, such that these responses are less available for other, unrelated actions (Hommel et al., 2001).

Experiment 3: Delayed Reproduction

One limitation of Experiments 1 and 2 was that mental practice was immediately followed by rhythm execution. This type of "preperformance imagery" (Morris et al., 2005) is often used in sports, before athletes engage in a difficult performance, and can be understood as an explicit and strategic form of movement preparation (e.g., Jeannerod, 1995, 1994; Lotze & Halsband, 2006). However, it raises the question whether the negative compatibility effect truly emerges from mental practice. An alternative is that the effects merely arose because participants anticipated using this body part for the subsequently execution of the rhythm.

Experiment 3 therefore attempts to replicate the results in a situation in which mental practice and execution do not follow one another immediately. Participants now mentally practiced two rhythms, one after the other, before they executed both of them (in the same order as they practiced them). Thus, Experiment 3 separates the mental practice of a rhythm and its execution by a different task (either the mental practice of another rhythm, or the actual execution of another rhythm). Replicating the prior effects would support the notion that the effects are related to mental practice with a body part, rather than the anticipation of an imminent motor response. In addition, it would extend our data to cases in which mental practice is separated from execution by another task and time interval.

Method

Participants.   Twenty-two volunteers (nine male, age range: 19–40 years) took part in the experiment. All other aspects of the participant selection were identical to Experiments 1 and 2. Five participants did not meet the inclusion criterion of fewer than 20% of trials with invalid responses/rhythms.

Materials and apparatus. Materials and apparatus were identical to Experiment 2.

Procedure and design. Experiment 3 differed to the previous experiment in that only 40 (instead of 80) experimental trials were presented. However, these trials now consisted of four (instead of two) phases: mental training of the first rhythm, mental training of the second rhythm, execution of the first rhythm, and execution of the second rhythm. The timing and presentation order in the different phases corresponded to the mental practice and execution phases of the previous experiments. Again, a low or high sound was played 5,000; 5,500; 6,000; or 6,500 ms after the start of either the first or the second mental practice interval, and participants responded to these sounds by either pressing both feet or both hand response keys. In the two execution intervals, participants again saw the description of the two rhythms and produced them as quickly as possible.

Analysis. 5.1% of trials were excluded because they contained "too early" responses or because the press of both response devices was not detected. For the analysis of RTs, error trials (2.1%) as well as trials with RTs that fell outside three standard deviations of the mean RT for responses with this body part (1.2%) were additionally excluded.

Results

The data were analyzed with repeated measures $2 \times 2 \times 2$ ANOVA, with the factors Response Effector (foot, hand), Imagery Effector (foot, hand), and Rhythm (first rhythm, second rhythm). The analysis of error rates (Figure 3, left panel) revealed neither a main effect of Imagery Effector, $F(1, 16) = 1.75$, $p = .204$, $\eta_p^2 = .10$, Response Effector, $F(1, 16) = 0.80$, $p = .38$, $\eta_p^2 = .05$, or Rhythm, $F(1, 16) = 3.77$, $p = .07$, $\eta_p^2 = .19$. However, as before, there was a significant interaction of Imagery Effector and Response Effector, $F(1, 16) = 7.61$, $p = .014$, $\eta_p^2 = .32$, again taking the form of a negative compatibility effect. No other effect was significant (all $F < 1$). Most important, there was no evidence for a three-way interaction of Response Effector, Imagery Effector, and Rhythm, $F(1, 16) = 0.003$. Indeed, planned comparisons confirmed that the interaction of Response Effector and Imagery Effector was present for both the mental practice of both the first,

$F(1, 16) = 3.71$, $p = .072$, $\eta_p^2 = .19$, and the second rhythm, $F(1, 16) = 6.97$, $p = .018$, $\eta_p^2 = .30$ (for separate analyses of each effector, see supplemental materials).

Again, the analysis of RTs (Figure 3, right panel) only revealed a main effect of Response Effector, $F(1, 16) = 19.4$, $p < .001$, $\eta_p^2 = .55$, and of Rhythm, $F(1, 16) = 14.0$, $p = .002$, $\eta_p^2 = .47$. No other main effect or interaction was significant (all $F < 1.5$). In particular, as in the previous experiments, the analysis of the RTs did not reveal an interaction of Imagery Effector and Response Effector, $F(1, 16) = 0.49$, $p = .494$, $\eta_p^2 = .03$. Moreover, the size of the compatibility effects in RTs and Error Rates were positively correlated ($r = .29$, ns), ruling out speed accuracy trade-offs.
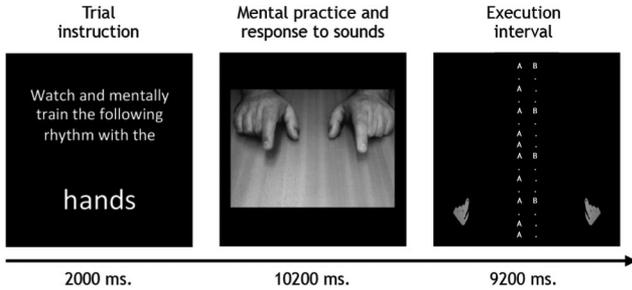
Discussion

The data again showed that participants made fewer errors when the body parts used for responding and for mentally practicing the rhythms were different rather than the same. This negative compatibility effect was found even though mental practice and execution were separated by a different task (the mental practice or execution of a different rhythm). The negative compatibility effects therefore do not only emerge because participants plan to use this body part for an imminent motor response. Rather, it reveals a specific effect of utilizing a body part in mental practice, such that it is less available for other responses, consistent with the idea that mental practice relies on planning-related motor processes.

Experiment 4: Imitation Learning

The findings of Experiment 1 to 3 are in stark contrast to the typical results from prior studies on stimulus response compatibility that report facilitatory effects of action-related stimuli on performing a similar response. For example, observing hand and foot actions facilitates responses with the same body parts (Bach & Tipper, 2007; Bach et al., 2007), even when observed and executed motor movements are not identical (Gillmeister et al., 2008). However, these prior experiments differed from ours in at least two respects. First, whereas in these prior studies the actions were directly presented, in ours they had to be internally generated, based on a symbolic rhythm description. Second, in the previous
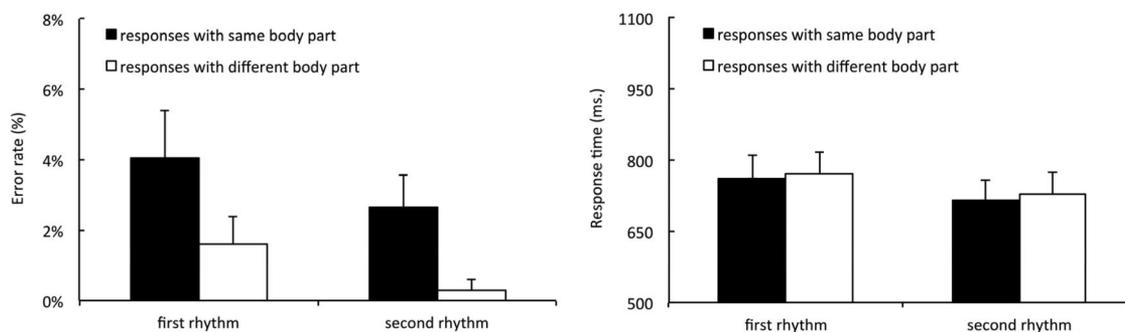
Figure 3. Error rates (left panel) and response times (right panel) in Experiment 3. In each panel, the two left bars show the responses during mental practice of the first rhythm, and the bars on the right show responses during mental practice of the second rhythm. The black bars show responses with the same body part that is used for mental practice, while the white bars show responses with the different body part. Error bars show the standard error of the mean.

Trial instruction | Mental practice and response to sounds | Execution interval

Watch and mentally train the following rhythm with the

hands

2000 ms.   10200 ms.   9200 ms.

Figure 4. Illustration of the trial sequence. The trial instruction (left panel) informed participants about the body part that would be used in the following rhythm. They then watched and mentally trained the demonstrated rhythm (middle panel) and responded with hands or feet to sounds played after 5,000; 5,500; 6,000; or 6,500 ms after the start of this interval. In the execution interval (right panel) they executed the rhythm.

studies, the actions the participants observed were completely task irrelevant, while in the present experiment the mentally practiced actions formed the basis of actions that had to be later executed. As noted above, various theorists (e.g., Hommel et al., 2001; Schuch & Koch, 2004; Stoet & Hommel, 1999) have proposed that features that are part of such action plans are not available for other processing (leading to negative compatibility effects), in contrast to when the same features are part of an incidentally observed stimulus (leading to positive compatibility effects; for reviews, see Hommel et al., 2001; Thomaschke et al., 2012).

To distinguish whether the negative compatibility effects are due to imagery or due to the requirement of establishing motor plans for subsequent performance, we converted the paradigm into an imitation paradigm. There is evidence that imitation is not based on a mere copying of the observed motor act but is based on action planning: Imitators typically use a motor act most appropriate given their own action capabilities and understanding of the action goal, even if it differs from the observed behavior (see Csibra, 2007 for an overview). In the mental practice interval of Experiment 5, participants therefore were not presented with the previous symbolic description of the rhythm, but now watched a rhythm that was tapped by another person. As before, they had to use this demonstration to mentally practice the rhythm in order to perform

it as quickly and accurately as possible later. They responded with hands or feet to a sound that was played to them while they watched and practiced. The difference to Experiments 1 to 3 is that participants did not have to generate an imagined rhythm but could derive it from the other person's movements, similar to prior work on action observation. If, in Experiments 1 to 3, the negative compatibility effects emerge because the eliciting stimuli were only imagined, then these effects should not be observed here and may even turn into positive effects, because the actions are explicitly presented as in other studies on action observation and stimulus response compatibility. If, however, the negative compatibility effects emerge because the body parts were part of a mentally rehearsed action plan, then the same negative compatibility effects should be observed here.

Method

Participants. Thirty-four students (nine male, age range: 18–27 years) took part in the experiment. All other aspects of the participant selection were identical to the previous experiments. Seven participants were excluded as they produced more than 20% invalid responses/rhythms.

Materials and apparatus. The apparatus was identical to the previous experiments. In addition to the symbolical rhythm descriptions, videos of another person tapping the rhythms were shot. The rhythms played by the person were the same as the rhythms used in the symbolic rhythm descriptions in Experiment 3. Thus, there were 20 videos of a person tapping the rhythms with the foot and 20 videos of a person tapping the rhythms with the hand. All movies were 9 s long. They showed the frontal view of the actor, cropped such that either only his hands and arms or feet were visible (see Figure 4).

Procedure and design. The procedure was based on Experiment 2. The course of each trial was identical to this experiment, with the exception that the symbolic rhythm descriptions in the mental practice interval were replaced with the movie stimuli of the same rhythms (see Figure 5, middle panel). Participants were instructed to watch these videos and use them to prepare the rhythms. In the execution interval, the symbolic rhythm descriptions were shown as in Experiment 2, and participants were again
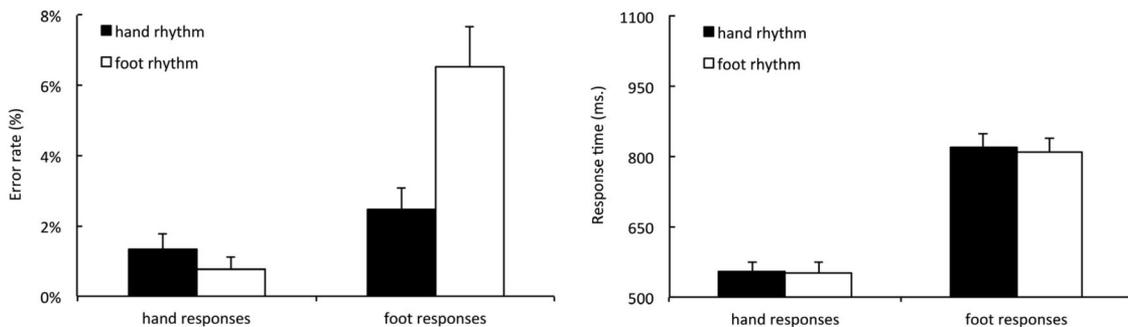
Figure 5. Error rates (left panel) and response times (right panel) in Experiment 4. In each panel, the two left bars show the data for responses with the hand, and the two right bars show responses with the feet. The black bars show responses while hand rhythms were mentally practiced, and the white bars show responses while foot rhythms were practiced. Error bars show the standard error of the mean.

instructed to mentally practice for as quick and accurate rhythm performance as possible.

Analysis. 1.4% of trials were excluded because they contained "too early" responses or because the press of both response devices was not detected. For the analysis of RTs, error trials (2.8%) as well as trials with RTs that fell outside three standard deviations of the mean RT for responses with this body part (0.5%) were additionally excluded.

Results

RTs and Error Rates were analyzed with separate 2×2 ANOVAs with the repeated measures factors Imagery Effector (foot, hand) and Response Effector (foot, hand). The analysis of error rates (Figure 5, left panel) revealed main effects of Imagery Effector, $F(1, 26) = 7.50$, $p = .011$, $\eta_p^2 = .22$, and of Response Effector, $F(1, 26) = 29.57$, $p < .001$, $\eta_p^2 = .53$, indicating that participants made fewer errors when responding with the hand than when responding with the foot, and when mentally practicing with the hand than the foot. Importantly, the interaction of Imagery Effector and Response Effector, $F(1, 26) = 11.39$, $p = .002$, $\eta_p^2 = .31$, again revealed a negative compatibility effect, with fewer errors being made with the body part not used for mental practice (for separate analyses of each effector, see supplemental materials).

The analysis of RTs (Figure 5, right panel) only revealed a main effect of Response Effector, $F(1, 26) = 349.69$, $p < .001$, $\eta_p^2 = .93$. The main effect of Imagery Effector and the interaction were not significant ($F = 1.16$ and $F < 1$, respectively). The size of the compatibility effects in RTs and error rates were slightly negatively correlated ($r = -.13$, ns).

Discussion

Experiment 4 revealed a continuity between learning from symbolic rhythm descriptions in Experiments 1 and 3 and learning from somebody else's actions in the present experiment. As in the earlier experiments, participants made mode errors when having to use a body part that was already engaged in mental practice, compared to a body part that was not. This finding demonstrates that the negative compatibility effect did not emerge because the movements were merely imagined, rather than being directly observed. Rather, what unifies all three experiments that yielded negative compatibility effects was that participants had to use the presented stimuli—be it videos or symbolic rhythm descriptions—to formulate a motor plan for later execution. Our finding is therefore consistent with the idea that generation of such a motor plan involves a binding of motor codes to action goals such that these codes are less available for other, unrelated responses (e.g., Hommel et al., 2001).

Experiment 5: No Mental Practice

Experiment 5 was designed to verify that the negative compatibility effects observed in Experiments 1 to 4 indeed reflect the mental practice component of the task, rather than other, confounding task aspects. For example, the effects could have been brought about by the visual presentation of hands or feet in the mental practice interval, when the model used these body parts to tap the rhythm (Experiment 4), or when they served as reminder

stimulus of which body part to train the rhythm with (Experiments 1 to 3). Of course, compatibility effects evoked by such stimuli are usually positive and not negative as was found here (Bach et al., 2007; Gillmeister et al., 2008). Moreover, these effects are typically found directly after stimulus onset but not after prolonged exposure (such as the 5 to 6 s to the onset of the sounds used here). Nevertheless, Experiment 5 was designed to fully control for the possibility that the negative compatibility effects are due to such unrelated task aspects.

Participants were exposed to exactly the same stimuli as in Experiment 4 (observation learning) but now were not instructed to mentally practice the viewed rhythms. Rather, their task was to merely memorize the rhythm tapped by the other person, so that they would be able to decide, in the second phase of each trial, whether the rhythm was the same or different to a symbolic rhythm description. Thus, rather than requiring the transformation of somebody else's action into one's own action plan, this task requires a transformation of somebody else's action into a symbolic description. As such, Experiment 5 keeps visual stimulation and task relevance constant, but eliminates the mental practice component of the task.

While memorizing the rhythms, participants again made speeded responses with either feet or hands in response to the task-unrelated sounds, to test whether this control task would similarly engage body part specific motor processes. If the negative compatibility effects found in Experiments 1 to 4 are due to the formation of an action plan, they should be eliminated in the current experiment. If, however, the negative compatibility effects are brought about by unrelated task aspects (e.g., the presence of hands and feet in the stimuli), then the same effects should be observed here.

Method

Participants. Thirty-three students (seven male; age range: 18–24 years) took part in the experiment. As before, participants were excluded when no valid button presses were recorded in more than 20% of trials. Participants were also excluded when their performance in the same/difference task was indistinguishable from chance (<60% correct), or too few verbal responses were recorded (<80%). As in the previous experiments, these criteria therefore capture both aspects of successful task performance: rhythm memorization and responses to the sounds. Of the 33 participants tested, six participants met these criteria, leading to an exclusion rate comparable to those in the previous experiments (Experiment 1, 4/20; Experiment 2, 5/23; Experiment 3, 5/22; Experiment 4, 7/34).

Materials and apparatus. The material and apparatus was identical to Experiment 4, with the exception that a microphone was additionally used to record the participants' verbal responses via Presentation's (http://www.neurobs.com) sound threshold detection logic.

Procedure and design. The procedure was based on Experiment 4. A movie of another person tapping a rhythm was presented in the first phase of each trial. Participants were instructed to watch this movie and to memorize the rhythm so that they would recognize it later. Participants again pressed either both foot or both hand buttons when they heard one of the two tones in this first "memorization" phase of the trials. In the second phase, partici-

pants were then shown a symbolic rhythm description (as used in the previous experiments) of either the same or a different rhythm. Their task was to merely state verbally whether this symbolic rhythm stimulus was "same" or "different" to the rhythm video they had just observed. The timing of these two phases across each trial was the same as in Experiment 4. However, as participants required less time to make their verbal same/different judgments than tapping the rhythm, we increased the number of trials (from 80 to 120), so that overall experiment times were similar. The results below are reported for the full 120 trials, but they are statistically identical when only the first 80 trials are analyzed.

Analysis. As before, the analysis focused on the responses to the task-unrelated sounds. 2.6% of trials were excluded because they contained "too early" responses or because the press of both response devices was not detected. For the analysis of RTs, error trials (2.3%) as well as trials with RTs that fell outside three standard deviations of the mean RT for responses with this body part (1.1%) were additionally excluded.

Results

As before, RTs and error rates were analyzed with separate 2×2 ANOVAs with the repeated measures factors Imagery Effector (foot, hand) and Response Effector (foot, hand; see Figure 6). The analysis of error rates revealed main effects of Response Effector, $F(1, 26) = 16.46, p < .001, \eta_p^2 = .39$, indicating that participants made fewer errors when responding with the hand than when responding with the foot. However, there was no effect of Response Effector, $F(1, 26) = 0.17, p = .686, \eta_p^2 < .01$. Moreover, in contrast to all previous experiments, the interaction of Imagery Effector and Response Effector was not significant, $F(1, 26) = 0.043, p = .837, \eta_p^2 < .01$. Moreover, comparing the size of compatibility effects between Experiments 4 and 5, which were identical with regard to visual stimulation, revealed a marginally significant difference ($t = 1.78; p = 081$).

The analysis of RTs only revealed a main effect of Response Effector, $F(1, 26) = 96.60, p < .001, \eta_p^2 = .79$. The main effect of Imagery Effector and the interaction were not significant ($F < 1$, for both).

Discussion

Experiment 5 shows that the previously recorded negative compatibility effects are due to the requirement to mentally practice the presented rhythms, and not just due to unrelated stimulus or task aspects (such as the presence of hands and feet in the visual stimulation). All these general task demands were kept identical in Experiment 5, while the need for mental practice was removed. We found that this manipulation eliminated the negative compatibility effects, linking them to mental practice rather than these unrelated task aspects. The effects therefore support the hypothesis that mental practice—like action planning—involves a binding of action features to action goals, making them less available to unrelated processes (e.g., Hommel et al., 2001).

Post Hoc Analyses

Do spontaneous motor responses reflect the activated action plans? Participants sometimes produced overt motor responses before the imperative sound cues were played. These "too early" trials were excluded from the main analysis but can be seen as a potential further indicator of the engagement of body-part-specific motor systems when mentally practicing the rhythms. To test whether these responses indeed reflect the spontaneous outflow of body-part-specific motor activation, we tested whether they were more likely to be made with the body part with which the rhythm had to be mentally practiced. As only few participants made these responses in each experiment (see Table 1), the comparison was run across all participants that produced "too early" responses across Experiment 1 to 4 in order to increase power. As expected, across experiments, participants were more likely to make "too early" responses with the body part used for mental practice compared with the other body part, $t(25) = 1.86, p = .037$. As seen in Table 1, the pattern held numerically for each of the four experiments and was marginally significant for Experiments 2 and 3 when tested separately. Of course, these results need to be interpreted with caution, as they only satisfied conventional significance thresholds ($p < .05$) but were part of several post hoc analyses. Nevertheless, they provide some indication that our tasks effectively engaged motoric mental practice processes that were
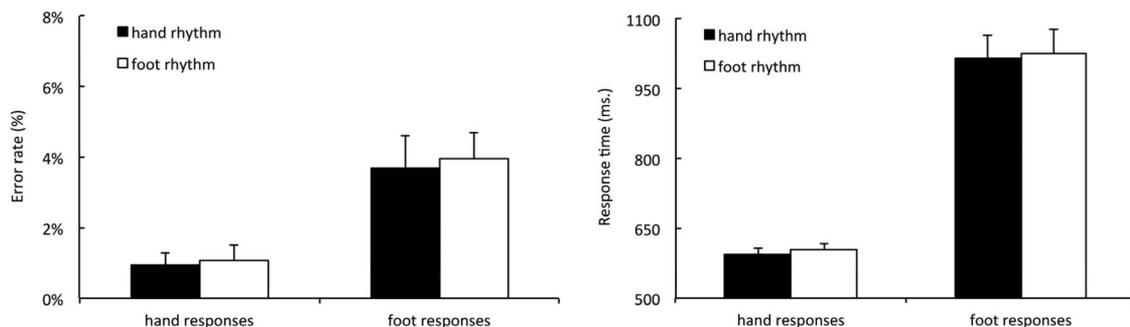

Figure 6. Error rates (left panel) and response times (right panel) in Experiment 5. In each panel, the two left bars show the data for responses with the hand, and the two right bars show responses with the feet. The black bars show responses while hand rhythms were mentally practiced, and the white bars show responses while foot rhythms were practiced. Error bars show the standard error of the mean.

Table 1
*Spontaneous Motor Responses During Mental Practice
Across Experiments*

Experiment	Same body part (%)	Different body part (%)	n	t	p
1 (from memory)	1.4	0.3	5	1.69	.166
2 (immediate production)	1.5	0.2	7	2.30	.061
3 (delayed production)	2.0	1.1	6	2.07	.093
4 (imitation)	1.6	0.6	8	1.10	.308

specific enough to sometimes accidentally trigger overt motor behavior.

Response inhibition or resource competition? An important question is what process the negative compatibility effects reflect. We interpreted these effects in terms of action planning processes, which "bound" the required body parts to the plans of producing the rhythm (e.g., Hommel et al., 2001) and rendered them less available for unrelated actions (the responses to the sounds). Alternatively, however, the negative compatibility effects could reflect inhibitory processes that prevent the formulated motor plans from activating overt motor responses, until required by the task. Indeed, if motor imagery engages execution-related processes then there need to be processes that inhibit the spontaneous outflow of motor activity during mental practice (e.g., James, 1890; Vogt, 1996; for fMRI evidence, see Solodkin et al., 2004).

One way to distinguish between these possibilities is to relate the negative compatibility effects to the spontaneous motor outflow during mental practice (the "too early" responses analyzed above). The resource competition and motor inhibition accounts make different predictions of how these spontaneous motor outputs should be related to the negative compatibility effects. According to the motor inhibition view, those participants that show the strongest negative compatibility effects when responding to the sounds should be the *least likely* to produce an overt motor response in the mental practice interval. The reason is that if the negative compatibility effects reflect an inhibition of spontaneous motor responses, then those participants that inhibit more should produce less motor output. The reverse is the case for the resource competition view. On this view, those participants with the strongest negative compatibility effects are seen as the participants that have formulated the strongest motor plans in the mental practice interval. They should therefore be the *most likely* to mistakenly execute this action plan and show "too early" responses with the body part used for mental practice.

The results favor the resource competition view. We computed the correlation between each participant's negative compatibility effect with their tendency to produce a motor response before the sounds were played with the body part used for mental practice (relative to responses with the other body part). As before, to increase power, this correlation was computed across all 26 participants in Experiments 1 to 4, who produced button presses before the sounds were played (after standardizing the effects for each experiment). Indeed, a highly significant negative correlation emerged ($r = -.63$, $p < .001$), indicating that those participants with the strongest negative compatibility effects were more—rather than less—likely to make an anticipative motor response with the body part used for mental practice. Negative correlations

were also observed when each experiment was analyzed separately (Experiment 1 [memory], $r = -.91$, Experiment 2 [fast responses], $r = -.47$, Experiment 3 [delayed responses], $r = -.30$, Experiment 4 [imitation], $r = -.86$). This correlational analysis therefore supports the view that the negative compatibility effects do not reflect the attempt to inhibit spontaneous motor outflow, but the formulation of an action plan that requires the "binding" of an effector to the action plan so that it is less available for other, unrelated responses but which can sometimes "leak out" and cause overt motor behavior.

Do responses with the same body part affect the ability to mentally practice the rhythms? The effects described so far reflect the effect of mental practice on the concurrent execution of unrelated responses. However, if mental practice and overt responses rely on overlapping mechanisms, then the opposite influence might be present as well: The hand and foot responses participants make to the sounds could affect how well they are able to mentally practice the rhythms. In other words, mental practice of the rhythms might be easier or harder depending on whether it was interrupted by a response made with the same or with a different body part. Although not the primary focus of this investigation, such reverse effects of action on cognition have been demonstrated before (e.g., Bach & Tipper, 2007; Müsseler & Hommel, 1997; Symes, Ottoboni, Tucker, Ellis, & Tessari, 2010; Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008; Tipper & Bach, 2008; Topolinski, 2012). They are often less robust and less often investigated than the typical compatibility effects of a stimulus on a response but are typically taken as strong evidence that motor activations play a causal—rather than epiphenomenal—role in the concurrent task (Hommel et al., 2001).

To assess the influence of overt responses on mental practice, we assessed how well participants played the rhythms afterward, depending on whether participants responded with the same or different body parts during mental practice. Two variables were created to assess the participants' performance. The first variable, *play time*, measured the speed with which participants produced the rhythms. For each rhythm played by a participant, we subtracted the time of the first button press in the execution interval from the last button press. The second variable, *deviance*, measured the accuracy of participants' performance. This was computed as the average of two submeasures. First, we measured the difference between the number of beats that the participants produced and the number of beats that were required for this particular rhythm, as a percentage of the total rhythm length. Second, we assessed whether the participants' relative frequency of presses with the left and right buttons corresponded to the relative frequency of left and right presses required by the rhythm, again as a percentage of total rhythm length. For these analyses, trials in which the button presses of the participants deviated by 50% or more from the required button presses were excluded, as well as trials in which participants took longer than 12 s to play the rhythm, or in which there was a pause between two button presses longer than 2 s.

A consistent numerical pattern across experiments was revealed for the deviance measure. As can be seen in Table 2, in all four experiments, participants tapped the rhythms more accurately when they had utilized the same body parts for responding to the sounds and for mental practice, compared to trials in which they used a different body part. This difference was highly significant

Table 2

Deviance and Play Time Depending on Whether Mental Practice Was Interrupted by a Response With the Same or a Different Body Part

Experiment	Deviance (%)		Play time (ms)	
	Same	Different	Same	Different
1 (from memory)	5.2	5.8	4,677	4,674
2 (speeded production)	3.1	4.0	3,247	3,247
3 (delayed production)	6.3	6.9	3,227	3,181
4 (imitation)	1.4	1.8	5,107	5,104

when data were pooled across experiments to increase power, $t(77) = 2.66$, $p = .009$. When performance was compared for each experiment separately, a significant difference was apparent for Experiment 2, $t(17) = 2.67$, $p = .016$, and a marginally significant difference for Experiment 4, $t(26) = 1.61$, $p = .059$, but not for Experiment 1, $t(15) = 1.41$, $p = .150$, and Experiment 3, $t(16) = 0.71$, $p = .487$.

As can be seen in Table 2, the play time measure did not reveal a consistent pattern across experiments. There was no significant difference, either when performance in both conditions was compared across experiments to increase power, $t(77) = 0.68$, $p = .500$, or in any of the single experiments: Experiment 1, $t(15) = 0.056$, $p = .956$; Experiment 2, $t(17) = 0.00$, $p = .998$; Experiment 3, $t(26) = 1.34$, $p = .20$; Experiment 4, $t(26) = 0.01$, $p = .994$.

Thus, the analysis of the rhythm performance reveals a consistent positive compatibility effect, at least when the data are pooled across experiments. Participants tapped the rhythms more accurately when their prior mental practice was interrupted by a button press that corresponded to the body part used in their motor plan, compared to a different body part. These data therefore show, first, that the processes in the mental practice intervals are indeed functionally related to successful rhythm performance. Second, they reveal that the success of mental practice depends on concurrent motoric activity, arguing against the idea that motoric engagement is epiphenomenal, or that it reflects activity not directly associated with mental practice (e.g., mere action-unrelated activation of body part concepts).

General Discussion

The current study tested whether mental practice of motor skills relies on body-part-specific motor processes involved in physical action execution. Participants mentally practiced complex rhythms with their feet or hands while making concurrent responses with either the same or different body parts. In four experiments, we found a direct influence of mental practice on these unrelated responses. It took the form of a negative compatibility effect, making it harder for participants to respond with the body part concurrently used in mental practice. Thus, while mentally practicing a rhythm with the hand participants were more likely to make accidental responses with the foot. While mentally practicing with the foot, they were more likely to accidentally respond with the hand.

This is the first behavioral study to reveal such a direct effect of mental practice on overt motor behavior. It therefore supports the view that mental practice is, at least partially, enactive and draws upon body part specific motor processes. In addition, it provides new insights about the nature about this motor involvement. The negative compatibility effects observed here are not consistent with the view that mental practice gives rise to the same subthreshold activation of low-level motor systems as the passive observation of action. Across studies and experimental paradigms, positive compatibility effects are typically observed, where viewing of action-related stimuli facilitates—rather than impairs—the execution of motorically similar responses (for reviews, see Hommel et al., 2001; Kornblum et al., 1990). Viewing hand and foot actions, for example, facilitates unrelated responses with the same body parts (Bach & Tipper, 2007; Bach et al., 2007; Gillmeister et al., 2008).

This difference does not simply emerge because, here, the actions were imagined while in the other studies they were directly observed. Positive compatibility effects are observed even when people imagine action-related stimuli (e.g., Bach et al., 2010; Tlauka & McKenna, 1998; Tucker & Ellis, 2001), and, in Experiment 4 here, the same negative compatibility effects were obtained even when the to-be-practiced foot and hand rhythms were not imagined but directly observed. Rather, the negative compatibility effects are in line with the view that our mental practice task specifically draws upon higher level action planning processes (cf. Hommel et al., 2001; Koch, Keller, & Prinz, 2004; Thomaschke et al., 2012). These processes allow actors to establish concrete plans for motor execution, by "binding" the different features an action needs to be successful—speed, direction of motion, or, here, the sequence of button presses with a certain body part—into unified plans for action. This binding allows even complex movements to be coordinated across effector systems, but, at the same time, renders the involved features less accessible for other responses. For example, it has been found that simply planning a left or right response makes it harder to make responses in the same direction, and planning to use a body part impairs the use of the same body part for another response (Stoet & Hommel, 1999; for similar effects, see Hübner & Druey, 2006; Schuch & Koch, 2004, 2010). Such effects are found as long as actions are planned but not executed, confirming their origin in planning rather than execution processes (Wühr & Müsseler, 2001).

Our data therefore suggest that mental practice is based on such planning-related motor processes. During mental practice, these processes may allow actors to develop complex plans for action that are aligned with both their goals and the (anticipated) demands of the performance situation. Several additional aspects of our results support such an involvement of planning related processes in mental practice. First, if the negative compatibility effects indeed reflect the formation of action plans, then they should be obtained only as long as the task requires participants to develop concrete plans for eventual execution. Indeed, across experiments, negative compatibility effects were found as long as the presented rhythms were the basis of subsequent motor performance, irrespective of whether this happened immediately after practice (Experiments 1, 2, and 4) or only after an intervening task (Experiment 3). However, as soon as the rhythms were not the basis of a future action of the participants—the condition under which positive compatibility effects are typically observed in other stimulus response compatibility paradigms—these effects were completely eliminated (Experiment 5).

Second, another feature of planning accounts is that the integration of features into action plans, while preventing their use for other responses, will benefit the execution of current plans. Such an effect was revealed, first, in the supplemental experiment (see online supplemental material), which confirmed that mentally practicing the rhythms indeed not only improves subsequent motor planning processes (as measured by time to initiate the rhythms) but motoric execution itself (measured by the time to execute the complete rhythm), replicating prior work on mental practice (Wohldman et al., 2007, 2008). Second, and more important, such an effect was revealed by analysis of the spontaneous motor responses participants sometimes made during mental practice. We found that those participants with the strongest negative compatibility effects were the most likely to accidentally press a response key during mental practice. Importantly, these responses were made with the body part concurrently used for mental practice, consistent with the idea that they reflect action plans that participants "forgot" to inhibit. Although post hoc, these data therefore confirm that mental practice indeed has two coupled effects on overt motor behavior: it prevents the use of the relevant action features in other unrelated responses, and, at the same time, facilitates the execution of the current plan (cf. Hommel et al., 2001).

Finally, an interesting finding was that our compatibility effects were only found in errors, not RTs, therefore reflecting the selection of an inappropriate effector for responding to the sounds (e.g., feet instead of hands). Effects only in errors—or only in RTs, for that matter—are typically seen as the ends of a continuum, where task factors bias participants toward either an optimization of response times or accuracy. In our study, various unspecific factors may have contributed to such a bias: (a) Participants did not receive feedback for either errors or too-slow responses, such that errors went unnoticed in many cases, and participants were not forced to make faster responses. (b) Even though participants were instructed to respond as quickly and accurately as possible to the sounds, the mental practice task was described as the primary task; subjects were instructed to not let this task be disrupted by the unrelated responses. (c) Due to the high demands of the primary task, response times to the sounds are unusually slow and reflect the average of two bimanual or bipedal responses, further obscuring any RT effects.

In addition to these unspecific task factors, however, the effect in errors/effector selection could also be taken as further evidence for a planning-origin of our effects. Effector selection is one of the earliest stages of motor planning, and changes in effector-specific readiness potentials are seen long before movements are initiated, and before other planning stages take part (see Bernier, Cieslak, & Grafton, 2012, for recent evidence). Effector selection rates have been a measure of choice in recent action planning/binding experiments (e.g., Dutzi & Hommel, 2009). For our study, although post hoc, the effect in error rates could therefore be taken as further indication that the overlap between physical action and mental practice happens on the level of action planning rather than physical action execution.

An interesting question is how the present data relate to the observation that actors either take a first-person perspective during mental practice and focus on the expected movement sensations, or practice in a more abstract manner focusing primarily on the intended outcomes in the third-person perspective (e.g., Lorey et al., 2009). This distinction is mirrored by current theories of action planning, which assume that actions can be planned on multiple levels, either using "proximal" action features (i.e., primarily first-person features related to the actor's body) or using more "distal" features that focus on the results to be achieved, rather than the movements itself (e.g., Hommel et al., 2001). As such, our finding of an engagement of body part specific motor-processes suggests a reliance on the former proximal codes in our task (Stinear et al., 2006; Voisin, Mercier, Jackson, Richards, & Malouin, 2011), and anecdotal reports from our participants support this notion. Future research will more directly explore this potential relationship between findings of mental practice and action planning, specifically testing whether the involvement of proximal motor codes can be linked to first-person kinaesthetic imagery.

An Action Planning Account of Mental Practice

Due to its role in novice and expert motor performance, mental practice is an important research focus in sports psychology and education. However, not much progress has been made in specifying the underlying processes, which are often conceptualized as either symbolic (Driskell et al., 1994; Minas, 1978; Sackett, 1934) or as deeply rooted in execution-related processes: emerging from a subliminal activation of the motor apparatus that allows actors to play through the sensations going along with the actions (Jacobson, 1930; Jeannerod & Frak, 1999). By linking mental practice to the planning processes that form the interface between higher level "cognitive" and lower level motor processes, our proposal suggests a unification of these approaches. As during action planning, mental practice may allow actors to formulate concrete plans for action that specify how the actions should look and feel if carried out. Subsequent rehearsal allows these "movement images" to be sharpened and refined, so that they can drive motor execution more effectively and are aligned with both the goals of the individual and the demands of the performance situation.

Because such planning views incorporate aspects of both symbolic and enactive accounts of mental practice, they allow us to integrate several conflicting findings in the literature and resolve several debates. A key example is the finding that that mental practice primarily benefits skills with cognitive components (e.g., Feltz & Landers, 1983; Hird et al., 1991; Ryan & Simons, 1983) but also has direct effects on motor execution and physiological variables (e.g., Wohldmann et al., 2007, 2008; Yue & Cole, 1992). While enactive theories struggle to account for the cognitive benefits, symbolic accounts have problems explaining motor or physiological benefits (for discussion, see Moran, Campbell, Holmes, & MacIntyre, 2012). Action planning accounts, however, can account for both. The cognitive benefits are in line with the notion that action planning is particularly beneficial if several sets of complex action sequences have to be coordinated, or integrated with varying environmental demands. Physiological or execution-related benefits, in contrast, can be explained because the purpose of action planning is effective execution. If mental practice allows existing movement plans to be sharpened and refined, they will become more effective drivers of later lower level motor processes. Indeed, the reported manual strength gains after mental practice, for example, are not due to changes to the actual muscles, but due to more effective signals reaching them (Ranganathan, Siemionow, Liu, Sahgal, Yue, 2004; Yue & Cole, 1992). Moreover, the strength gains are tied to the vividness of imagery during

mental practice, consistent with the idea that sharper mental images generated during mental practice are better drivers of intended motor output (Reiser et al., 2011).

A second debate concerns the factors influencing the benefits of mental practice on performance. Motor theories naturally account for the larger benefits of first-person (rather than third-person) and kinesthetic imagery, where people imagine the actions as if they would be carrying them out (Lorey et al., 2009; Stinear et al., 2006). After all, this type of imagery most closely mirrors the sensory feedback that would emerge from a subliminal activation of the motor system. However, those theories struggle to account for effects of imagery that are not motor-related. It is known, for example, that mental practice has stronger benefits when imagery also captures the environmental, cognitive and emotional aspects of the performance situation (for a review, see Holmes & Collins, 2001). As the purpose of action planning is precisely the mediation between the higher level goals, environmental influences and the action possibilities of the individual, planning-related theories can account for the influences of such extraneous ("distal") variables, ensuring that the resulting action plans properly take into account the demands of the performance situation (for an extensive review of the role of distal variables in action planning, see Hommel et al., 2001; for use affective action features in action planning, see Eder, Müsseler, & Hommel, 2012).

Finally, understanding mental practice in terms of action planning-related processes allows us to integrate conflicting findings from neuroimaging studies. First, while neuroimaging studies are generally consistent with the idea that action-related structures are engaged in motor imagery, there is considerable debate whether this activation reflects execution-related processes. For example, when amputees report the feeling of being able to move their amputated hand, both the phenomenological experience and brain activation corresponds more closely to actual movement execution than to movement imagery, even though kinesthetic feedback is controlled (Raffin et al., 2012). Such dissociations are no surprise for planning accounts, which assume that any overlap should be found for planning but not execution related structures. Indeed, primary motor cortex activation—closely linked to physical motor execution—is not consistently found across studies on motor imagery. In contrast, premotor cortex activation, much more closely aligned to action planning, is consistently observed (for a review, see Lotze & Halsband, 2006). Moreover, a recent fMRI study has directly compared imagery-related brain activity with both preparatory and execution related activity. As predicted from the present findings, motoric activation during imagery was aligned with planning, not execution (Hanakawa et al., 2008).

Second, our data may have something to say on why these motoric activations during motor imagery are sometimes inhibitory (rather than facilitatory). These inhibitory effects are typically discussed in terms of a prevention of spontaneous motor outflow (e.g., Solodkin et al., 2004; Tipper & Bach, 2008). Our present data suggest that they may be better interpreted as a more natural consequence of an action planning process that involves a binding of motor features to a not-yet-executed motor plan such that these features are not available for unrelated responses. Indeed, the brain areas involved in these suppressive effects on motor output during imagery—the supplemental motor area and the parietal visuomotor areas (Solodkin et al., 2004)—are also crucial nodes in action planning networks (e.g., Hanakawa et al., 2008). Moreover, the

supplemental motor area in particular has been implicated in action-effect learning and may therefore represent specifically the intended features of an action plan (Elsner et al., 2002; Melcher et al., 2008).

Finally, our data shed light on whether the premotoric activation is merely an epiphenomenon, rather than a crucial component of motor imagery (for discussion, see Jeannerod, 1994; Mahon & Caramazza, 2008). Our data argue against this possibility. First, the fact that the inhibitory effects are linked to the execution of an action plan argues against a mere motor outflow process and suggest a goal-directed linkage to action goals. Second, and more important, our paradigm also revealed effects of motor execution on mental practice, such that subsequent execution was facilitated when mental practice was interrupted by a response with the same body part. Such effects are typically seen to be strong evidence for an involvement of motor structures in cognition, as they reflect a "backward" influence, where activation in the motor system influences task performance. They would not be expected if motor systems would not play a crucial role in the task. For our study, they therefore suggest that the motoric activations during mental practice play a fundamental role in mental practice and are functionally linked to the improvement of the trained motor skill. Of course, the effects observed here need to be interpreted with caution, as they were not as robust as the negative compatibility effects and our paradigm was not designed to investigate these action-to-mental practice effects. Nevertheless, the presence of these effects provides evidence that motor structures are required for mental practice.

It is an open question why these action-to-practice effects were in the opposite direction as the compatibility effects found in the responses to the sounds. Along with certain models of motor imagery (Jeannerod, 1995) and mental practice (Beisteiner, Höllinger, Lindinger, Lang, & Berthoz, 1995), we speculate that whereas response initiation requires that the required action codes are not already used for another goal, imagery can benefit from concurrent kinaesthetic feedback that strengthens the underlying movement representations. Although testing these ideas is beyond the scope of the present article, it is important to note that identical dissociations had been observed in the original studies on action effect binding (Stoet & Hommel, 1999). While planning a response inhibits the use of similar motoric features in other responses, executing an action provides additional activation to—and facilitates the execution of—movement plans that are currently held active, and share some of the action's features. As such, while having to be clarified by further research, these effects of motor execution on mental practice nevertheless (a) highlight the functional role of action related processes for successful mental practice and (b) further support the proposed link to prior research on action planning.

Linking Mental Practice and Imitation Learning

While Experiments 1 to 3 link action planning to mental practice, Experiment 4 extends this link to imitation, a research focus of anthropology and developmental psychology. Imitation is a key means for transmitting knowledge, both within and between generations. It allows observers to put themselves into other people's shoes, vicariously experience the outcome of their actions and learn from their experience, enabling them to later reproduce the

behaviors and achieve the same goals. It is often assumed that humans can imitate because watching others does give rise to a subtle "resonance" of the motor apparatus, which manifests as a tendency to nonstrategically and nonconsciously copy others' behavior and body postures (Chartrand & Bargh, 1999; for reviews, see Heyes, 2011; van der Wel et al., 2013; Wang & Hamilton, 2012). It is assumed that, during imitation proper, observers would similarly "tap into" this motor activation to reproduce the desired behaviors.

Experiment 4 challenges this idea by revealing that the general motor resonance evoked by incidentally observing others is absent when people watch others with the express purpose to imitate. Instead, the to-be-imitated action features were less— rather than more—available for unrelated responses. Experiment 4 therefore suggests that watching somebody to imitate is more akin to mental practice than automatic imitation and gives rise to the same binding effects. Imitating an observed action may therefore similarly involve the purposeful selection of intended action features and "binding" them into an action plan. The only difference is that in mental practice these features were self-generated, while in imitation they could be extracted directly from the other person's action.

The implied difference between imitation proper and more automatic forms of imitation is consistent with recent theoretical developments in infant research. There, imitation is similarly distinguished from its more automatic counterparts, and understood as a goal-directed process, which serves the acquisition of knowledge about which sequences of motor behaviors achieve a particular outcome (Csibra, 2007; Heyes, 1993). For example, when intending to imitate, infants do not – as motor resonance accounts would imply—merely copy the observed movements, but focus on the action's goal: They faithfully reproduce the motor behavior only, when they believe it to be crucial for goal achievement. Otherwise, they use an action that is most rational in terms of their own action capabilities and their understanding of the relevant causal relationships (e.g., Bekkering et al., 2000; Gergely, Bekkering, & Király, 2002). Moreover, these forms of imitation are not automatic. They emerge from an intentional stance for learning, which is triggered either by the motivation to attain desired action consequences (for a review, see Elsner, 2007), or by "natural pedagogy," the various cues adults give to signal to the infant that there is something to learn (for an overview, see Csibra & Gergely, 2009).

Experiment 4 therefore suggests that this distinction between automatic and intentional imitation is mirrored on the motor level. Whereas incidentally watching somebody generally primes the motor apparatus for similar movements, in goal-directed imitation, these activations are linked to a goal. Only motor behaviors that subserve this goal will be facilitated, while others—even when motorically similar—are inhibited. This hypothesis could be tested in typical mimicry experiments, where it is found that observation of another person elicits a tendency to perform similar movements (e.g., Chartrand & Bargh, 1999). We predict that, when the other person is just incidentally watched, their movements (e.g., face rubbing) should evoke not only to automatic imitation of the specific movements but also a more general tendency to use the same body part, even for unrelated movements (e.g., finger tapping). In contrast, when the goal is to watch the other person for later imitation, such a general activation of the body parts should

be absent. Any movements that are observed should capture specifically the to-be-imitated behavior.

Conclusions

This study revealed that mental practice—the mental rehearsal of motor skills to improve subsequent performance—builds upon processes involved in action planning. Like action planning, mental practice involves a binding of response codes to action plans, such that they are less available for other, unrelated responses. Moreover, the study revealed a continuity of processing between mental practice and imitation learning, suggesting that the same planning-related motor processes underlie both.

References

Annett, J. (1995). Motor imagery: Perception or action. *Neuropsychologia, 33,* 1395–1417. doi:10.1016/0028-3932(95)00072-B

Arora, S., Aggarwal, R., Sirimanna, P., Moran, A., Grantcharov, T., Kneebone, R., . . . Darzi, A. (2011). Mental practice enhances surgical technical skills: A randomized controlled study. *Annals of Surgery, 253,* 265–270. doi:10.1097/SLA.0b013e318207a789

Bach, P., Griffiths, D., Weigelt, M., & Tipper, S. P. (2010). Gesturing meaning: Non-action words activate the motor system. *Frontiers in Human Neuroscience, 4,* 214. doi:10.3389/fnhum.2010.00214

Bach, P., Peatfield, N. A., & Tipper, S. P. (2007). Focusing on body sites: The role of spatial attention in action perception. *Experimental Brain Research, 178,* 509–517. doi:10.1007/s00221-006-0756-4

Bach, P., & Tipper, S. P. (2007). Implicit action encoding influences personal-trait judgments. *Cognition, 102,* 151–178. doi:10.1016/j.cognition.2005.11.003

Beisteiner, R., Höllinger, P., Lindinger, G., Lang, W., & Berthoz, A. (1995). Mental representations of movements: Brain potentials associated with imagination of hand movements. *Electroencephalography & Clinical Neurophysiology, 96,* 183–193. doi:10.1016/0168-5597(94)00226-5

Bekkering, H., Wohlschlaeger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology, 53,* 153–164.

Bernier, P. M., Cieslak, M., & Grafton, S. T. (2012). Effector selection precedes reach planning in the dorsal parietofrontal cortex. *Journal of Neurophysiology, 108,* 57–68.

Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception and Performance, 32,* 210–225. doi:10.1037/0096-1523.32.2.210

Brass, M. Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition, 44,* 124–143. doi:10.1006/brcg.2000.1225

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76,* 893–910. doi:10.1037/0022-3514.76.6.893

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 1673–1692. doi:10.1037/0096-1523.25.6.1673

Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Attention and performance XXII: Sensorimotor foundations of higher cognition* (pp. 435–459). Oxford, England: Oxford University Press.

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences, 13,* 148–153. doi:10.1016/j.tics.2009.01.005

Decety, J. (1996). Do imagined and executed actions share the same neural substrate? *Cognitive Brain Research, 3,* 87–93. doi:10.1016/0926-6410(95)00033-X

Decety, J., & Michel, F. (1989). Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and Cognition, 11,* 87–97. doi:10.1016/0278-2626(89)90007-9

Dechent, P., Merboldt, K. D., & Frahm, J. (2004). Is the human primary motor cortex involved in motor imagery? *Cognitive Brain Research, 19,* 138–144. doi:10.1016/j.cogbrainres.2003.11.012

de Lange, F. P., Roelofs, K., & Toni, I. (2008). Motor imagery: A window into the mechanisms and alterations of the motor system. *Cortex, 44,* 494–506. doi:10.1016/j.cortex.2007.09.002

Driskell, J. E., Copper, C., & Moran, A. (1994). Does mental practice enhance performance? *Journal of Applied Psychology, 79,* 481–492. doi:10.1037/0021-9010.79.4.481

Dutzi, I. B., & Hommel, B. (2009). The microgenesis of action-effect binding. *Psychological Research, 73,* 425–435.

Eder, A. B., Müsseler, J., & Hommel, B. (2012). The structure of affective action representations: Temporal binding of affective response codes. *Psychological Research, 76,* 111–118. doi:10.1007/s00426-011-0327-6

Elsner, B. (2007). Infants' imitation of goal-directed actions: The role of movements and action effects. *Acta Psychologica, 124,* 44–59. doi:10.1016/j.actpsy.2006.09.006

Elsner, B., Hommel, B., Mentschel, C., Drzezga, A., Prinz, W., Conrad, B., & Siebner, H. (2002). Linking actions and their perceivable consequences in the human brain. *NeuroImage, 17,* 364–372. doi:10.1006/nimg.2002.1162

Feltz, D., & Landers, D. (1983). The effects of mental practice on motor skill learning and performance: A meta-analysis. *Journal of Sport Psychology, 5,* 25–57.

Feltz, D., Landers, D., & Becker, B. (1988). *A revised meta-analysis of the mental practice literature on motor skill learning.* Washington, DC: National Academy Press.

Georgopoulos, A. P., & Massey, J. T. (1987). Cognitive spatial-motor processes. *Experimental Brain Research, 65,* 361–370, doi:10.1007/BF00236309

Gergely, G., Bekkering, H., & Király, I. (2002). Developmental psychology: Rational imitation in preverbal infants. *Nature, 415,* 755. doi:10.1038/415755a

Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based priming of body parts: A study of action imitation. *Brain Research, 1217,* 157–170. doi:10.1016/j.brainres.2007.12.076

Grouios, G. (1992). The effect of mental practice on diving performance. *International Journal of Sport Psychology, 23,* 60–69.

Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain Sciences, 27,* 377–396. doi:10.1017/S0140525X04000093

Guillot, A., Lebon, F., Rouffet, D., Champely, S., Doyon, J., & Collet, C. (2007). Muscular responses during motor imagery as a function of muscle contraction types. *International Journal of Psychophysiology, 66,* 18–27. doi:10.1016/j.ijpsycho.2007.05.009

Hall, E. G., & Erffmeyer, E. S. (1983). The effect of visuomotor rehearsal with videotaped modeling on free throw accuracy of intercollegiate female basketball players. *Journal of Sport Psychology, 5,* 343–346.

Hanakawa, T., Dimyan, M. A., & Hallett, M. (2008). Motor planning, imagery, and execution in the distributed motor network: a time-course study with functional MRI. *Cerebral Cortex, 18,* 2775–2788.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46,* 999–1010. doi:10.1006/anbe.1993.1281

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin, 137,* 463. doi:10.1037/a0022288

Hinshaw, K. (1991). The effects of mental practice on motor skill performance: Critical evaluation and meta-analysis. *Imagination, Cognition and Personality, 11,* 3–35. doi:10.2190/X9BA-KJ68-07AN-QMJ8

Hird, J. S., Landers, D. M., Thomas, J. R., & Horan, J. J. (1991). Physical practice is superior to mental practice in enhancing cognitive and motor task performance. *Journal of Sport & Exercise Psychology, 13,* 281–293.

Holmes, P., & Collins, D. (2001). The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology, 13,* 60–83. doi:10.1080/10413200109339004

Hommel, B. (2011). The Simon effect as tool and heuristic. *Acta Psychologica, 136,* 189–202. doi:10.1016/j.actpsy.2010.04.011

Hommel, B. (2013). Ideomotor action control: On the perceptual grounding of voluntary actions and agents. In W. Prinz, M. Beisert, & A. Herwig (Eds.), *Action science: Foundations of an emerging discipline* (pp. 112–136). Cambridge, MA: MIT Press. doi:10.7551/mitpress/9780262018555.003.0005

Hommel, B., Müsseler, M., Aschersleben, A., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24,* 849–878. doi:10.1017/S0140525X01000103

Hübner, R., & Druey, M. (2006). Response execution, selection, or activation: What is sufficient for response-related repetition effects under task shifting? *Psychological Research, 70,* 245–261. doi:10.1007/s00426-005-0219-8

Hughes, G., Desantis, A., & Waszak, F. (2013). Mechanisms of intentional binding and sensory attenuation: The role of temporal prediction, temporal control, identity prediction, and motor prediction. *Psychological Bulletin, 139,* 133–151. doi:10.1037/a0028566

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology, 60,* 653–670. doi:10.1146/annurev.psych.60.110707.163604

Ionta, S., Fourkas, A. D., Fiorio, M., & Aglioti, S. M. (2007). The influence of hands posture on mental rotation of hands and feet. *Experimental Brain Research, 183,* 1–7. doi:10.1007/s00221-007-1020-2

Jacobson, E. (1930). Electrical measurements of neuromuscular states during mental activities: I. Imagination of movement involved skeletal muscle. *American Journal of Physiology, 91,* 567–608.

James, W. (1890). *Principles of psychology.* London, England: Macmillan. doi:10.1037/11059-000

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences, 17,* 187–245. doi:10.1017/S0140525X00034026

Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia, 33,* 1419–1432. doi:10.1016/0028-3932(95)00073-C

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage, 14,* S103–S109. doi:10.1006/nimg.2001.0832

Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology, 9,* 735–739. doi:10.1016/S0959-4388(99)00038-0

Jowdy, D. P., Murphy, S. M., & Durtschi, S. (1989). *An assessment of the use of imagery by elite athletes: Athlete, coach and psychologist perspectives.* Unpublished report to the United States Olympic Committee, Colorado Springs, CO.

Koch, I., Keller, P., & Prinz, W. (2004). The ideomotor approach to action control: Implications for skilled performance. *International Journal of Sport and Exercise Psychology, 2,* 362–375. doi:10.1080/1612197X.2004.9671751

Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus–response compatibility—A model and taxonomy. *Psychological Review, 97,* 253–270. doi:10.1037/0033-295X.97.2.253

Landauer, T. K. (1962). Rate of implicit speech. *Perceptual and Motor Skills, 15,* 646. doi:10.2466/pms.1962.15.3.646

Lorey, B., Bischoff, M., Pilgramm, S., Stark, R., Munzert, J., & Zentgraf, K. (2009). The embodied nature of motor imagery: The influence of posture and perspective. *Experimental Brain Research, 194,* 233–243. doi:10.1007/s00221-008-1693-1

Lotze, M., & Halsband, H. (2006). Motor imagery. *Journal of Physiology—Paris, 99,* 386–395. doi:10.1016/j.jphysparis.2006.03.012

Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., . . . Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of Cognitive Neuroscience, 11,* 491–501.

Mackay, D. G. (1981). The problem of rehearsal or mental practice. *Journal of Motor Behavior, 13,* 274–285. doi:10.1080/00222895.1981 .10735253

Macuga, K. L., & Frey, S. H. (2012). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *NeuroImage, 59,* 2798–2807. doi:10.1016/j.neuroimage .2011.09.083

Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology—Paris, 102,* 59–70. doi:10.1016/j .jphysparis.2008.03.004

Melcher, T., Weidema, M., Eenshuistra, R. M., Hommel, B., & Gruber, O. (2008). The neural substrate of the ideomotor principle: An event-related fMRI analysis. *NeuroImage, 39,* 1274–1288. doi:10.1016/j.neuroimage .2007.09.049

Miller, K. J., Schalk, G., Fetz, E. E., den Nijs, M., Ojemann, J. G., & Rao, R. P. (2010). Cortical activity during motor execution, motor imagery, and imagery-based online feedback. *Proceedings of the National Academy of Sciences of the United States of America, 107,* 4430–4435. doi:10.1073/pnas.0913697107

Minas, S. C. (1978). Mental practice of a complex perceptual motor skill. *Journal of Human Movement Studies, 4,* 102–109.

Moran, A. P., Campbell, M., Holmes, P., & MacIntyre, T. (2012). Mental imagery, action observation and skill learning. In N. Hodges & M. A. Williams (Eds.), *Skill acquisition in sport: Research, theory and practice* (pp. 94–111). Sussex, United Kingdom: Routledge.

Morris, T., Spittle, M., Watt, A. P., & Fletcher, S. (2005). Technical aids to imagery. In T. Morris, M. Spittle, & A. P. Watt (Eds.), *Imagery in sport* (pp. 237–266). Champaign, IL: Human Kinetics.

Müsseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 23,* 861–872. doi:10.1037/0096-1523.23.3.861

Naito, E., Kochiyama, T., Kitada, R., Nakamura, S., Matsumura, M., Yonekura, Y., & Sadato, N. (2002). Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. *The Journal of Neuroscience, 22,* 3683–3691.

Noel, R. (1980). The effect of visuo-motor behavior rehearsal on tennis performance. *Journal of Sport Psychology, 2,* 221–226.

Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., . . . di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. *The Journal of Neuroscience, 16,* 7688–7698.

Raffin, E., Mattout, J., Reilly, K. T., & Giraux, P. (2012). Disentangling motor execution from motor imagery with the phantom limb. *Brain, 135,* 582–595.

Ranganathan, V. K., Siemionow, V., Liu, J. Z., Sahgal, V., & Yue, G. H. (2004). From mental power to muscle power: Gaining strength by using the mind. *Neuropsychologia, 42,* 944–956. doi:10.1016/j.neuropsycho-logia.2003.11.018

Reed, C. (2002). Chronometric comparisons of imagery to action: Visualizing versus physically performing springboard dives. *Memory & Cognition, 30,* 1169–1178. doi:10.3758/BF03213400

Reiser, M., Büsch, D., & Munzert, J. (2011). Strength gains by motor imagery with different ratios of physical to mental practice. *Frontiers of Psychology, 2*(194). doi:10.3389/fpsyg.2011.00194

Richardson, A. (1967). Mental practice: A review and discussion (Part 1). *Research Quarterly, 38,* 95–107.

Ross, S. (1985). The effectiveness of mental practice in improving the performance of college trombonists. *Journal of Research in Music Education, 33,* 221–230. doi:10.2307/3345249

Roure, R., Collet, C., Deschaumes-Molinaro, C., Delhomme, G., Dittmar, A., & Vernet-Maury, E. (1999). Imagery quality estimated by autonomic response is correlated to sporting performance enhancement. *Physiology & Behavior, 66,* 63–72. doi:10.1016/S0031-9384(99)00026-8

Ryan, D., & Simons, J. (1983). What is learned in mental practice of motor skills. *Journal of Sport Psychology, 5,* 419–426.

Sackett, R. S. (1934). The influence of symbolic rehearsal upon the retention of a maze habit. *The Journal of General Psychology, 10,* 376–398.

Schuch, S., & Koch, I. (2004). The costs of changing the representation of action: Response repetition and response-response compatibility in dual tasks. *Journal of Experimental Psychology: Human Perception and Performance, 30,* 566–582. doi:10.1037/0096-1523.30.3.566

Schuch, S., & Koch, I. (2010). Response-repetition effects in task switching with and without response execution. *Acta Psychologica, 135,* 302–309. doi:10.1016/j.actpsy.2010.07.016

Simon, J. R. (1969). Reactions towards the source of stimulation. *Journal of Experimental Psychology, 81,* 174–176.

Simon, J. R. & Rudell, A. P. (1967). Auditory S-R compatibility: the effect of an irrelevant cue on information processing. *Journal of Applied Psychology, 51,* 300–304.

Solodkin, A., Hlustik, P., Elinor Chen, E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. *Cerebral Cortex, 14,* 1246–1255. doi:10.1093/cercor/bhh086

Steggemann, Y., Engbert, K., & Weigelt, M. (2011). Selective effects of motor expertise in mental body rotation tasks: Comparing object-based and perspective transformations. *Brain and Cognition, 76,* 97–105. doi:10.1016/j.bandc.2011.02.013

Stinear, C. M., Byblow, W. D., Steyvers, M., Levin, O., & Swinnen, S. P. (2006). Kinesthetic, but not visual, motor imagery modulates cortico-motor excitability. *Experimental Brain Research, 168,* 157–164. doi: 10.1007/s00221-005-0078-y

Stoet, G., & Hommel, B. (1999). Action planning and the temporal binding of response codes. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 1625–1640. doi:10.1037/0096-1523.25.6 .1625

Symes, E., Ottoboni, G., Tucker, M., Ellis, R., & Tessari, A. (2010). When motor attention improves selective attention: The dissociating role of saliency. *The Quarterly Journal of Experimental Psychology, 63,* 1387–1397. doi:10.1080/17470210903380806

Symes, E., Tucker, M., Ellis, R., Vainio, L., & Ottoboni, G. (2008). Grasp preparation improves change detection for congruent objects. *Journal of Experimental Psychology: Human Perception and Performance, 34,* 854–871. doi:10.1037/0096-1523.34.4.854

Thomaschke, R., Hopkins, B., & Miall, R. C. (2012). The planning and control model (PCM) of motorvisual priming: Reconciling motorvisual impairment and facilitation effects. *Psychological Review, 119,* 388–407. doi:10.1037/a0027453

Tipper, S. P., & Bach, P. (2008). Your own actions influence how you perceive other people: A misattribution of action appraisals. *Journal of Experimental Social Psychology, 44,* 1082–1090. doi:10.1016/j.jesp .2007.11.005

Tlauka, M., & McKenna, P. F. (1998). Mental imagery yields stimulus–response compatibility. *Acta Psychologica, 98,* 67–79. doi:10.1016/ S0001-6918(97)00050-4

Topolinski, S. (2012). The sensorimotor contributions to implicit memory, familiarity, and recollection. *Journal of Experimental Psychology: General, 141,* 260–281. doi:10.1037/a0025658

Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object recognition. *Visual Cognition, 8,* 769–800. doi:10.1080/13506280042000144

van der Wel, R. P. R. D., Sebanz, N., & Knoblich, G. (2013). Action perception from a common coding perspective. In K. Johnson & M. Schiffrar (Eds.), *People watching: social, perceptual and neurophysiological studies of body perception* (pp. 101–118). New York, NY: Oxford University Press.

Vogt, S. (1996). Imagery and perception-action mediation in imitative actions. *Cognitive Brain Research, 3,* 79–86. doi:10.1016/0926-6410(95)00032-1

Voisin, J. I., Mercier, C., Jackson, P. L., Richards, C. L., & Malouin, F. (2011). Is somatosensory excitability more affected by the perspective or modality content of motor imagery. *Neuroscience Letters, 493,* 33–37.

Wang, Y., & Hamilton, A. F. D. C. (2012). Social top-down response modulation (STORM): A model of the control of mimicry in social interaction. *Frontiers in Human Neuroscience, 6,* 153.

Weigelt, M., Ahlmeyer, T., Lex, H., & Schack, T. (2011). The cognitive representation of a throwing technique in judo experts:Technological ways for individual skill diagnostics in high performance sports. *Psychology of Sport and Exercise, 12,* 231–235. doi:10.1016/j.psychsport.2010.11.001

Winter, H. (2002, November 2). Coaches united in seeking the psychological edge. *The Telegraph.* Retrieved from http://www.telegraph.co.uk/

Wohldmann, E. L., Healy, A. F., & Bourne, L. E., Jr. (2007). Pushing the limits of imagination: Motor imagery for learning sequences and skill. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33,* 254–261. doi:10.1037/0278-7393.33.1.254

Wohldmann, E., Healy, A. F., & Bourne, L. E., Jr. (2008). A mental practice superiority effect: Less retroactive inhibition and more transfer than physical practice. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 823–833. doi:10.1037/0278-7393.34.4.823

Wohlschläger, A., & Wohlschläger, A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 397–412. doi:10.1037/0096-1523.24.2.397

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology, 11,* R729–R732. doi:10.1016/S0960-9822(01)00432-8

Wühr, P., & Müsseler, J. (2001). Time course of the blindness to response compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 27,* 1260–1270. doi:10.1037/0096-1523.27.5.1260

Yue, G., & Cole, K. J. (1992). Strength increases from the motor program: Comparison of training with maximal voluntary and imagined muscle contractions. *Journal Neurophysiology, 67,* 1114–1123.

Zimmermann-Schlatter, A., Schuster, C., Puhan, M. A., Siekierka, E., & Steurer, J. (2008). Efficacy of motor imagery in post-stroke rehabilitation: A systematic review. *Journal of Neuroengineering and Rehabilitation, 5,* 8. doi:10.1186/1743-0003-5-8